Anatomy, Distribution, Synonymy, and Systematic Relationships of *Atagema alba* (O'Donoghue, 1927) (Nudibranchia: Doridacea)

by

HANS BERTSCH¹

Biological Sciences, National University, San Diego, California 92106, U.S.A.

AND

TERRENCE M. GOSLINER

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. We illustrate the radula (with scanning electron microscopy) and the reproductive system of Atagema alba. We report the occurrence of this species from northwestern Baja California, Mexico (in addition to its known distribution in southern and central California, U.S.A.), confirm the identity of A. alba, and contrast A. alba with its known congeners. We discuss the problematic nature of using the degree of elaboration of the prostatic region to distinguish the Doridinae, Archidoridinae, and Discodoridinae.

INTRODUCTION

THE OPISTHOBRANCH SPECIES of the Pacific coast of California are fairly well known, but there still remain some taxonomic problems that require resolution (BEHRENS, 1980; MCDONALD & NYBAKKEN, 1981). During the past 20 years, various authors have proposed solutions to some of these (*e.g.*, STEINBERG, 1961, 1963; ROLLER, 1970; BEHRENS, 1984).

In contrast, one species has been given two synonyms in the past 20 years. Although the posthumous publication of MACFARLAND'S (1966) major monograph on western North American opisthobranchs resolved many problems, it also created duplication of scientific names. The editors of that monograph decided to publish MacFarland's names—even though they might be proliferating new synonyms—and leave it to future workers to resolve the nomenclatural problems. *Petelodoris spongicola* MacFarland, 1966, was thus introduced into the literature even though it is an obvious synonym of Atagema quadrimaculata Collier, 1963 (ROLLER, 1970). The identity of Glossodoridiformia alba O'Donoghue, 1927, had remained in doubt, and the species overlooked by most recent workers, until MCDONALD (1983:150-151) proposed that this species was synonymous with Atagema quadrimaculata.

In this paper we describe aspects of the anatomy of *Atagema alba* (O'Donoghue, 1927), extend its known range into Mexican waters, discuss its synonymy and distinguishing characteristics (comparing it with both the north-eastern Pacific opisthobranch fauna and its congeners), and discuss its subfamilial placement.

ANATOMY

Material Examined

One specimen, 38 mm long; subtidal, 13.7 m deep, on the exposed cliff face of a pinnacle at the outer entrance of a small cove at Arbolitos, in the Punta Banda area, south of Ensenada, Baja California, Mexico (31°42'N, 116°41'W); 2 December 1984; *leg.* H. Bertsch and T. Smith. The individual (Figure 1) was on a small rocky

¹ Mailing address: 6056 Beeman Avenue, North Hollywood, CA 91606, U.S.A.



Explanation of Figures 1 and 2

Figure 1. In situ underwater photograph of Atagema alba, 13.7 m depth, Arbolitos, Baja California (HB photograph).

Figure 2. Close-up of *Atagema alba* collected at Arbolitos (David Mulliner photograph).

ledge on which were numerous solitary corals, *Balano-phyllia elegans* Verrill, 1864. An obvious sponge food was not immediately visible; strong surge and currents prevented us from further searching.

External Anatomy

Atagema alba is an elongate dorid, strongly humped along the midline (Figure 1). It is whitish, with small blackgray flecks that give the animal a dirty appearance. The rhinophore sheaths form elevated, prominent cones around the proximal portions of each rhinophore. The branchiae project posteriorly from underneath 3 flat, posteriorly directed branchial lobes. There are broad, triangular, auriform tentacles, and a greatly exaggerated upper lobe to the bilabiate anterior foot margin.

The most diagnostic external features of this species (which O'Donoghue partly described or partly attributed to his specimen being damaged) are: the rhinophore sheath that forms a high cone (a generic character; see MAC-FARLAND, 1966:pl. 27, fig. 5, and our Figure 2); the broad, triangular, auriform tentacles; the extremely deep bilabiate nature of the anterior foot margin (see MAC-FARLAND, 1966: pl. 27, fig. 4) with an enlarged upper lobe; and the posteriorly pointing branchiae underneath 3 horizontal lobes ("giving the animal a superficial likeness to a phanerobranchiate form," O'DONOGHUE, 1927:88).

Radula

The radula consists of simply hamate, hooklike teeth (Figures 3, 4). The scanning electron micrographs illustrate the simple shape of these teeth, and the lack of any accessory denticles. The radular formula of our specimen from Mexico is 17 (26.0.26). O'Donoghue's holotype had a radular formula of 17-18 (25-26.0.25-26); Collier's specimen was 18 (18-19.0.18-19), and MacFarland's was 15 (20-23.0.20-23). The known composite radular formula of *A. alba* is 15-18 (17-26.0.17-26).

Reproductive System

The convoluted ampulla bifurcates distally into the short oviduct and elongate vas deferens. The vas deferens is round in cross section and prostatic proximally. It then narrows sharply and again widens into a muscular, ejaculatory segment. A distinct penial papilla is absent. The oviduct enters the albumen gland, the smallest portion of the female gland mass. The mucous gland is the largest portion of the mass. The mucous gland is ventral to and smaller than the membrane gland. The receptaculum seminis is saccate and muscular. From its base extend two ducts. The more proximal one enters the albumen gland near the entrance of the oviduct. The distal duct joins the duct of the thin-walled, spherical bursa copulatrix. Together these ducts form the vagina, which shares a common gonopore with the penis. The mucous gland empties

DISTRIBUTION

The known distribution of *Atagema alba* is from Point Pinos, in Monterey, California (MACFARLAND, 1966), to San Diego, California (COLLIER, 1963). Our specimen represents a southern range extension of over 100 km, and the first report of the species from Mexican waters. This extension is not surprising because the fauna of the northwest coast of Baja California is part of the Californian temperate faunal province (BERTSCH, 1983, 1985; BERTSCH & JOHNSON, 1983). *Atagema alba* is now known from central and southern California and northwestern Baja California (from Monterey, California, to Arbolitos, about 15 km south of Ensenada, Baja California, Mexico). It has been found in areas of strong surf or surge, from the extreme low intertidal to the shallow subtidal zones (MCDONALD, 1983; personal observations).

DISCUSSION

Comparison with Sympatric Doridaceans and Synonymy

Our recent collection of a specimen of Atagema alba prompted us to re-examine McDONALD's (1983) proposed synonymy. He had based the synonymy on the unique branchial arrangement and on a number of traits that are referable to several species (e.g., white ground color, small papillae on dorsum, and number of rhinophore lamellae). We decided to base our acceptance or rejection of his synonymy on a detailed comparison of Atagema alba with all other northeastern Pacific opisthobranch species (using as many anatomical characters as possible).

We were able to select 13 characteristics from O'DONOGHUE'S (1927:87-89) description that could give information about the specific identity of the organism, and then compared these with all known species of opisthobranchs from the American Pacific coast (BEHRENS, 1980; McDONALD & NYBAKKEN, 1981). Atagema quadrimaculata is the only species that exhibited all 13 characters.

The overwhelming concordance of Atagema quadrimaculata with the features described by O'Donoghue, and the incomplete agreement with any other species, led us to re-affirm the synonymy of Glossodoridiformia alba and Atagema quadrimaculata. The possibility that O'Donoghue's species has not been collected since its original description can be discarded because O'Donoghue's description fits known, recently collected specimens so well, and because the fauna of the central-southern California area is quite well known. Priority of the genus name Atagema necessitated the name change to Atagema alba. Hence, the synonymy is as follows:



Explanation of Figures 3 and 4

Figures 3, 4. Scanning electron micrographs of the radula of Atagema alba (specimen collected at Arbolitos). Magnification and scale on pictures (SEM's by TG).

Atagema quadrimaculata Collier, 1927 Petelodoris spongicola MacFarland, 1966

Collier's holotype specimen of Atagema quadrimaculata had been deposited in the collections of the California Academy of Sciences; through an oversight, the museum number was not given in the original publication. The holotype is catalogued as CASIZ No. 018182.

Comparison with Known Congeners

Species of the genus Atagema occur in the northern Pacific, the southwestern Pacific, and the eastern Atlantic (including the Mediterranean). The three Atlantic species all have five lobes to the pre-branchial flaps (whereas A. alba has three): Atagema gibba Pruvot-Fol, 1951, A. rugosa Pruvot-Fol, 1951, and A. africana Pruvot-Fol, 1953. These species were described with even less information than O'Donoghue used to name A. alba. They are brownish, and have more teeth per half row than does A. alba. The fingerlike oral tentacles of A. gibba are different than those found in A. alba. THOMPSON & BROWN (1974) and PERRONE (1983) further distinguish A. gibba and A. rugosa. Studying PRUVOT-FOL's (1953:76-77) description of A. africana suggests that further research on additional specimens from the original locality may show that this species is synonymous with an earlier named Atagema.

The New Zealand Atagema carinata (Quoy & Gaimard, 1832) can be distinguished from A. alba because of its pure white color, contrasting pale yellow-orange rhinophores and gills, and broadly oval (rather than elongate) body form (WILLAN & COLEMAN, 1984).

Atagema triphylla (Bergh, 1882) (type species by monotypy of Petelodoris) shares a number of characteristics with Atagema alba: shape of radular teeth, three pre-branchial lobes, white with brown speckling color, etc. Although it has a radular formula identical to that of the specimens MacFarland used to name Petelodoris spongicola, the described radula and body of A. triphylla are smaller. Bergh indicates that A. triphylla has brown coloration on the fine papillae, whereas MacFarland indicates that the brown coloration is between the papillae. The only known specimen of A. triphylla was collected in Japan. Although some eastern Pacific species are known to occur in Japan (e.g., BABA, 1937, Diaulula sandiegensis), the geographic separation (A. alba has not been collected north of central California) and anatomical differences are sufficient to prevent synonymizing these two species based on the available information. The identity of A. triphylla must await recent collections of Atagema from Japan.



Reproductive system of Atagema alba. Al, albumen gland; Am, ampulla; BC, bursa copulatrix; Ej, ejaculatory duct; Me, membrane gland; Mu, mucous gland; NO, nidamental opening; Pr, prostate; RS, receptaculum seminis; ζ , common gonopore.

Systematic Relationships

The systematic relationships among cryptobranch doridacean nudibranchs have traditionally been a source of confusion and difference of opinion. Familial and subfamilial divisions have been based largely upon differences in reproductive anatomy (ODHNER, 1926, 1939; THIELE, 1931; BURN, 1968; FRANC, 1968; SCHMEKEL & PORT-MANN, 1982). The degree of elaboration of the prostate and penial papilla has been used to distinguish between the Doridinae, Archidoridinae, and Discodoridinae.

The Doridinae was separated from the Archidoridinae by ODHNER (1926) but later (ODHNER, 1939) he combined the two subfamilies within the Doridinae. BURN (1968) transferred Austrodoris odhneri MacFarland, 1966, from the Doridinae to the genus Archidoris in the Archidoridinae. This alteration was made based on the fact that MacFarland's species possesses a prostatic region and has a small, but distinct, penial papilla. On the other hand, SCHMEKEL & PORTMANN (1982) described the reproductive system of Archidoris pseudoargus (Von Rapp, 1827). The specimen they depicted (fig. 7.9b) has a large penial papilla (as in Archidoris), but lacks a thickened prostatic region.

Atagema has been placed in the Archidoridinae by most authors (MACFARLAND, 1966, as *Petelodoris*; THOMPSON & BROWN, 1976, 1984; BEHRENS, 1980; MCDONALD, 1983) but has been placed in the Doridinae by others (ODHNER, 1939; ABBOTT, 1974). Atagema alba has a welldifferentiated, flattened prostatic region, distinct from the narrow, non-prostatic vas deferens of Arichidoris pseudoargus, and the prominently developed prostate of the Discodoridinae, such as Anisodoris nobilis (MACFARLAND, 1966:pl. 37, fig. 27).

The division of the subfamilies of the Dorididae and the distinction between the Doridinae and Archidoridinae, in particular, are certainly open to question. The fact that species that appear to be included in *Archidoris* differ in the elaboration of the prostate and penial papilla suggests that the separation of the subfamilies may be unwarranted. However, more detailed study of several taxa is required to determine the variability of these morphological characters. The type species of *Archidoris, Doris tuberculata* Cuvier, 1804, must be examined before meaningful conclusions can be drawn to determine subfamilial and generic limits.

ACKNOWLEDGMENTS

We thank Tom Smith for collecting assistance underwater and David Mulliner for his photograph of the *Atagema*.

LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold Company: New York. 663 pp.
- BABA, K. 1937. Opisthobranchia of Japan. 2. J. Dept. Agri. Kyushu Imper. Univ. 5(7):289-344.
- BEHRENS, D. W. 1980. Pacific coast nudibranchs. A guide to the opisthobranchs of the northeastern Pacific. Sea Challengers: Los Osos. 112 pp.
- BEHRENS, D. W. 1984. Notes on the tergipedid nudibranchs of the northeastern Pacific, with a description of a new species. Veliger 27(1):65-71.
- BERGH, L. S. R. 1882. Beiträge zur Kenntnis der japanischen Nudibranchien. II. Verh. Zool.-Bot. Gesell. Wien 31:219– 254.
- BERTSCH, H. 1983. Estudios de ecosistemas bentónicos a lo largo de la costa noroccidental de Baja California, Mexico: distribución y presa de varios invertebrados marinos. Ciencias Marinas 8(2):91-123.
- BERTSCH, H. 1985. An international reconnaissance expedition: marine zoogeography of Baja California Sur. Environment Southwest 508:18-23.
- BERTSCH, H. & S. JOHNSON. 1983. Zoogeografía comparativa de los opistobranquios (Mollusca: Gastropoda) con énfasis en la cuenca Pacífica (Hawaii y California): composición faunal, afinidades provinciales y densidad submareal. Ciencias Marinas 8(2):125–153.
- BURN, R. 1968. Archidoris odhneri (MacFarland, 1966) comb. nov., with some comments on the species of the genus on the Pacific coast of North America. Veliger 11(2):90-92.
- COLLIER, C. 1963. A new member of the genus Atagema (Gastropoda: Nudibranchia) a genus new to the Pacific northeast. Veliger 6(2):73-75.
- FRANC, A. 1968. Sous-classe des opisthobranches. In: P.-P.

Grassé (ed.), Traite de zoologie: anatomie, systematique, biologie. Tome V, Fasc. III:608-893.

- MACFARLAND, F. M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Calif. Acad. Sci. Mem. 6:1-546.
- MCDONALD, G. R. 1983. A review of the nudibranchs of the California coast. Malacologia 24(1-2):114-276.
- McDONALD, G. R. & J. W. NYBAKKEN. 1981. Guide to the nudibranchs of California. American Malacologists: Melbourne, Florida. 72 pp.
- ODHNER, N. H. 1926. Die Opisthobranchien. Further Zool. Res. Swedish Antarctic Exped. 1901-1903. II(1):1-100.
- ODHNER, N. H. 1939. Opisthobranchiate Mollusca from the western and northern coasts of Norway. Det Kgl. Norske Vidensk. Selsk. Skr. 1939(1):1–93.
- O'DONOGHUE, C. H. 1927. Notes on a collection of nudibranchs from Laguna Beach, California. J. Entom. Zool. Pomona Coll. 19:77-119.
- PERRONE, A. 1983. Record of Atagema rugosa Pruvot-Fol, 1951 (Opisthobranchia: Nudibranchia). J. Moll. Stud. 49(1):88.
- PRUVOT-FOL, A. 1951. Etude des nudibranches de la Méditerranée (2e partie). Arch. Zool. Exper. Gen. 88:1-80.
- PRUVOT-FOL, A. 1953. Etude de quelques opisthobranches de la côte Atlantique du Maroc et du Sénégal. Travaux de l'Institut Scientifique Cherifien, Ser. Zool. 2:1-105.
- QUOY, J. R. C. & J. P. GAIMARD. 1832-1833. Voyage de découvertes de l'Astrolabe ... pendant les années 1826-1829, sous le commandement de M. J. Dumont D'Urville. Zoologie 2:1-686.
- ROLLER, R. A. 1970. A list of recommended nomenclatural changes for MacFarland's "Studies of opisthobranchiate mollusks of the Pacific coast of North America." Veliger 12(3):371-374.
- SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres: Nudibranchia und Saccoglossa. Springer-Verlag: Berlin. x + 410 pp.
- STEINBERG, J. 1961. Notes on the opisthobranchs of the west coast of North America I. Nomenclatural changes in the order Nudibranchia (southern California). Veliger 4(2):57-63.
- STEINBERG, J. 1963. Notes on the opisthobranchs of the west coast of North America—III. Further nomenclatorial changes in the order Nudibranchia. Veliger 6(2):63-67.
- THIELE, J. 1931. Handbuch der systematischen Weichtierkunde 1(2):420-461.
- THOMPSON, T. E. & G. H. BROWN. 1974. Atagema gibba Pruvot-Fol, a doridacean nudibranch new to the British fauna. J. Conch. 28:223-237.
- THOMPSON, T. E. & G. H. BROWN. 1976. British opisthobranch molluscs, Mollusca: Gastropoda, keys and notes for the identification of the species. Synopsis of the British Fauna (new series), No. 8, Linn. Soc. London. 203 pp.
- THOMPSON, T. E. & G. H. BROWN. 1984. Biology of opisthobranch molluscs. Vol. 2. The Ray Society: London. 228 pp.
- WILLAN, R. C. & N. COLEMAN. 1984. Nudibranchs of Australasia. Australasian Marine Photographic Index: Sydney, Australia. 56 pp.